# THE WING-VENATION OF THE ORDER ISOPTERA. I.

## Introduction and the Family Mastotermitidae.

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(Plate xxi; eight Text-figures.)

### Introduction.

The Division of Economic Entomology of the Council for Scientific and Industrial Research of the Australian Commonwealth is divided up into Sections which correspond with the principal economic problems whose solutions are being attempted. One of the most important of these is the problem of Termites or so-called "White Ants". Throughout the whole Continent of Australia, these insects cause immense damage annually to timber and structures built of timber. The prevention of this damage is a matter of the utmost importance to the Commonwealth. The total annual loss due to Termites, in the destruction of growing trees, railway sleepers, telegraph posts and cross-arms, fences and weatherboard houses, not to mention damage done to fruit trees, stored products of various kinds and even, in some parts, to grass-lands, is estimated at fully one million pounds sterling.

The Section of Forest Insects Research, under the charge of Mr. G. F. Hill as Senior Entomologist, has placed this problem in the forefront of its programme, and is acting in close co-operation with the Division of Forest Products and also with the Commonwealth Forestry Bureau in an endeavour to minimize the losses arising from Termites.

An important part of this work consists of a systematic survey of the species found in Australia and neighbouring countries. In the course of this survey, a very large amount of valuable material has been collected together, including what is probably the largest amount of living material ever assembled, for use in the field testing plots and laboratory colonies.

The total number of described species of Termites in the whole world is now about 1,600. Of these, already about 150 have been described from Australia, while some seventy more are known but not yet named and described. Many species and several genera have been inadequately defined, often being based on a type series that is incomplete in the sense that it does not include all the castes. Genera have been defined on characters which fuller experience proves to be unreliable. The position at the present time is such that it appears almost impossible to determine what some of the economic forms really are. Without accurate determinations of genera and species, the literature on the economic side must inevitably become more and more full of errors, and it is already abundantly clear that a thorough revision of the classification of the Order is needed.

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To show how even the comparatively simple problem of the correct identity of two species may affect the economic problem, we need only mention the confusion which has arisen in the past between the two closely related species *Coptotermes lacteus* Frogg. and *C. flavus* Hill.  It has been widely believed that *C. lacteus*, well-known as the cause of much damage to weatherboard buildings and also as the builder of large dome-shaped mounds in the bush, also attacks standing forest trees.  Consequently, one method suggested for the protection of valuable forest reserves was the destruction of the mounds of this species.  But it is now known that the species which attacks living trees is the closely allied *C. flavus*, which, on present evidence, does not form mounds at all!  Hence the destruction of these mounds, though it would benefit anybody who wished to erect a weatherboard dwelling in the bush, would in no wise protect the standing timber.

A further difficulty arises owing to the unreliability of some of the characters at present used in classification.  We have even noted an extreme case in which right and left wings from the same individual were classified into two distinct genera based on venational differences!  It seems obvious that, even if no characters of value can be discovered in the worker castes, reliable genera in this Order should now be strongly based on a correlation of characters taken from the alate forms and the soldiers, and not merely from one or the other.

The accumulation of an immense mass of excellently preserved material offers an unrivalled opportunity for such a study, and the possession of large numbers of living forms allows more particularly of the carrying out of a piece of work which must surely yield particularly good results in the systematic field, viz., a study of the wing-tracheation of the developing nymphs.  Mr. Hill and I have therefore agreed that we will undertake a joint piece of research, in which Mr. Hill's part will be to study the whole field of Australian Isoptera in order to find reliable characters for classification other than in the wing-venation, while I shall confine myself to a study of the developing wing-tracheation of the nymphs and the resulting wing-venation of the imagines.  While following up these two lines of study we intend to write a series of papers correlating the results of our work.

I propose to divide my own share of the work into four parts, based on the four recognized families within the Order, viz., Mastotermitidae, Calotermitidae, Rhinotermitidae and Termitidae.  The present Part deals with the family Mastotermitidae.

### The Venation of the Family Mastotermitidae.

The moment that one begins to consider the venational problem presented by the Order Isoptera, there comes into view the archaic Australian genus *Mastotermes* Frogg., at the present time only represented by a single species, the Giant Termite of Northern Australia, *Mastotermes darwiniensis* Frogg. This species causes immense losses over a wide belt of Northern Australia.  In many respects it may be said to hold the record amongst all insects for its powers of attack.  Not only does it destroy all kinds of prepared timber except a few immune varieties but it does immense damage to living trees in the forest, to fruit trees and ornamental trees, and to various kinds of stored products.  It has even been recorded as eating through lead-piping, and a remarkable instance is well authenticated in which it ate out the insides of some bonzoline billiard balls in a Darwin hotel! The winged forms swarm round the lights at periods ranging from late in November to early in February.  Though winged forms and workers are very

abundant, nymphs are not so often met with, and many colonies appear to consist only of workers, soldiers and neoteinics. No true queen has yet been found, but it is believed that such does exist.

The most important piece of work requisite for a sound understanding of the wing-venation of Isoptera is undoubtedly a study of the nymphal tracheation in the genus *Mastotermes*. The opportunity to carry this out came to me in 1929 during a short visit to Townsville. Mr. Hill had informed me that all the fences and many of the trees in the hospital grounds of that city had been badly infested with *Mastotermes* when he was stationed there, and he asked me to send him supplies of living insects for his laboratory colonies in Canberra. When I reached Townsville in July, 1929, I found that the last of the wooden fencing had just been removed and was being replaced by concrete in order to save the heavy costs of almost continual renewals; so I turned my attention to the trees in the grounds. The hospital authorities very kindly gave me permission to cut down a large Poinciana tree which appeared to be badly infested. The tree was cut down and sawn into sections, and the roots were completely excavated. It was found that no connection existed between the *Mastotermes*-colony and the outside world, but that practically every part of the tree was tunnelled, and the roots were bored out right to their very ends. The resulting census of this colony showed that the tree contained about 100,000 workers in various stages of development, some 3,000 soldiers, and a few small and isolated colonies of a species of *Cryptotermes* in some of the branches. Nymphs of *Mastotermes* were especially sought for, but only two could be found, both in the penultimate instar and both living in galleries situated in rather small branches. It seems clear, therefore, either that nymphs are not produced every season in large numbers, or else that this colony, large as it was, was only an offshoot of some larger underground nest in which most of the nymphs were living.

The two nymphs were dissected in one of the laboratories at the School of Tropical Medicine in Townsville, where facilities for the work were kindly placed at my disposal by Dr. Richards. I wish here to thank him for his kindness and assistance. The results obtained will be described in detail in this Part.

As no nymphs of the last instar could be found, and as Comstock had already (1918) figured tracheae as still existing in the vein-channels of the wings of the imago, a search was later on made amongst Mr. Hill's material for last instar nymphs preserved in alcohol. One specimen from Groote Eylandt, Gulf of Carpentaria, appeared to me to be in excellent condition for dissection. In the dissected wing-sheaths of this specimen, tracheae were found almost as perfect as in the living nymph. The resulting drawings are made use of in this Part.

For a study of the imaginal venation, I have had the use of a number of slides of wings lent by Mr. Hill, and have also examined complete specimens of both sexes in alcohol. My best thanks are due to Mr. Hill for this valuable assistance.

A number of attempts have already been made by various authors to determine the homologies of the wing-veins in the genus *Mastotermes* without reference to the tracheation of the nymphal wings.* There are, however, some obvious anomalies in the venational scheme which make a satisfactory solution difficult, as the following comparative table of results will show:

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* The paper by Claude Fuller entitled "The Wing Venation and Respiratory System of Certain South African Termites," *Ann. Natal Museum*, 1919, iv, pp. 19-102, does not, of course, include any reference to Mastotermitidae, but gives many figures of wing-tracheation in the other three families.

*Table Showing Comparative Results for Wing-venation of the Genus* Mastotermes.

| | Desneux, 1904. | Silvestri, 1909. | Holmgren, 1911. | Comstock, 1918. | Tillyard, 1926. | Tillyard, 1931. |
|---|---|---|---|---|---|---|
| Forewing only .. .. | Sc | — | C | $Sc_1$ | Sc | Sc |
| „ „ .. .. | — | — | C | $Sc_1$ | Sc | Sc |
| Both Wings .. .. | Sc | C | Sc | $Sc_2$ | Sc | Sc |
| „ „ .. .. | R | Sc | $R_1$ | $R_1$ | $R_1$ | $R_1$ |
| „ „ .. .. | R | Sc | $R_1$ | $R_2$ | $R_{2+3}$ | $R_{2+3}$ |
| „ „ .. .. | R | R | Rs | $R_3$ | $R_4$ | $R_4$ |
| „ „ .. .. | R | R | Rs | $R_4$ | $R_5$ | $R_5$ |
| „ „ .. .. | R | R | Rs | $R_5$ | $R_5$ | $R_5$ |
| „ „ .. .. | M | M | M | M | M | M |
| „ „ .. .. | Cu | Cu | Cu | Cu | $Cu_{1a}$ | $Cu_1$ |
| *Vena dividens* (fore-wing only) .. .. | A | A | A | Anal Furrow | $Cu_{1a}$ | $Cu_2$ |
| Homologous Vein (in hindwing only) .. | A | $A_1$ | A | 1st A | $Cu_{1a}$ | $Cu_2$ |
| Vein anterior to anal fold (h i n d w i n g only) .. .. .. | — | $A_2$ | Postanal | 2nd A | $Cu_{1b}$ | 1A |
| Vein along anal fold (hindwing only) .. | — | — | — | Anal Furrow | $Cu_2$ | $2A_1$ |
| Veins posterior to anal fold .. .. | — | A | Postanal | 3rd A | 1A | $2A_2$ |
| (hindwing only) .. | — | A | Postanal | 3rd A | 2A ⎫ 3A ⎭ | 3A |

*Note.*—The last column contains the results arrived at in the present paper. The most anterior vein of the wing is normally simple (except for small twigs) in the hindwing, but it is branched in the forewing; as there are usually two anterior branches of this vein separating off within the wing-stump of the forewing before the main branch, these are allowed for separately in the first two rows of the table.

Reviewing the above table, we note that there is absolute agreement amongst all the authors quoted in the case of one vein only, viz., the media. Opinions differ on all other important points, e.g., as to the presence or absence of a true costal vein apart from the subcosta, as to the limits of Sc, $R_1$ and Rs, as to the interpretation of the *vena dividens* of the forewing, and as to the limits of the anal venation and the composition of the veins of the anal lobe in the hindwing.

Apart from the present paper, Comstock is the only author who has made an attempt to utilize the wing-tracheation. Having no nymphs to work with, he nevertheless attempted to trace the tracheae in the veins of the imago. As a result, his conclusions come fairly close to those reached in the present paper through the study of the nymphal wing-tracheation.

I now propose to deal with (1) the wing-tracheation of the penultimate nymphal instar, (2) the wing-tracheation of the last nymphal instar, (3) the interpretation of the wing-venation of the imago in terms of the results so obtained, and (4) the problem of de-alation.
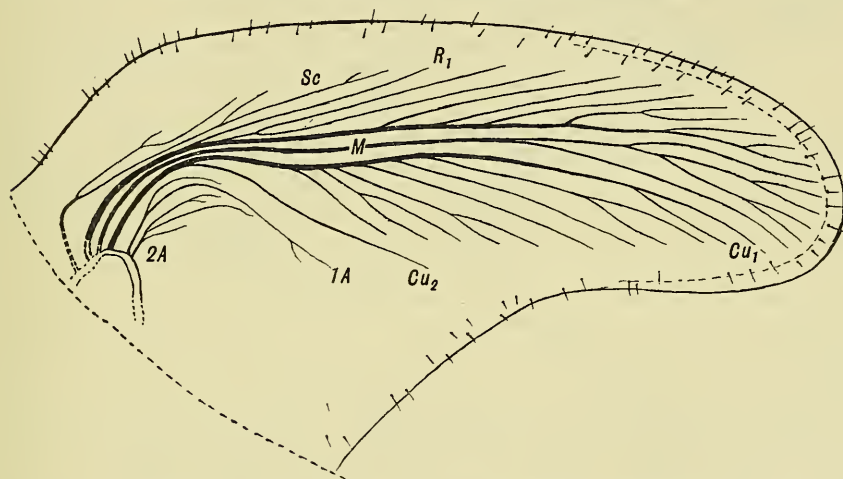
(1) *The Wing-Tracheation of the penultimate Nymphal Instar.* Text-figs. 1, 2.

The dissections of the wing-sheaths of the penultimate nymphal instar were made from freshly chloroformed material taken at Townsville, N.Q., by myself on 26th June, 1930. Only two nymphs were available. Text-figure 1 shows the tracheation of the forewing of one of these.

We note first of all the great breadth of the sheath, which, measured across the base where it was cut off, is almost exactly one-half of the total length.

Further, both anterior and posterior margins are very strongly arched, the former near the base, the latter about midway. This results in giving the impression that the wing-sheath began to grow in one direction and then turned more posteriorly. This impression is, I think, correct, as the position of the sheath with respect to the thorax strongly suggests that the basal part preserves to a considerable degree the original direction of a primitive paranotal expansion, and that, as this elongated, it tended to develop in a more posterior direction, as indicated by the distal portion. It would be very interesting to obtain the earlier instars of these nymphs in order to study the shape of the sheath in the successive instars from the first appearance of the wing-buds.

It is, unfortunately, almost impossible to dissect out the basal tracheal trunk complete, without badly disarranging the wing-tracheae, as it is rather deeply sunk in fat-tissue and not easy to see. I succeeded in preserving the posterior portion of it in the forewing, fortunately including therewith the actual origins
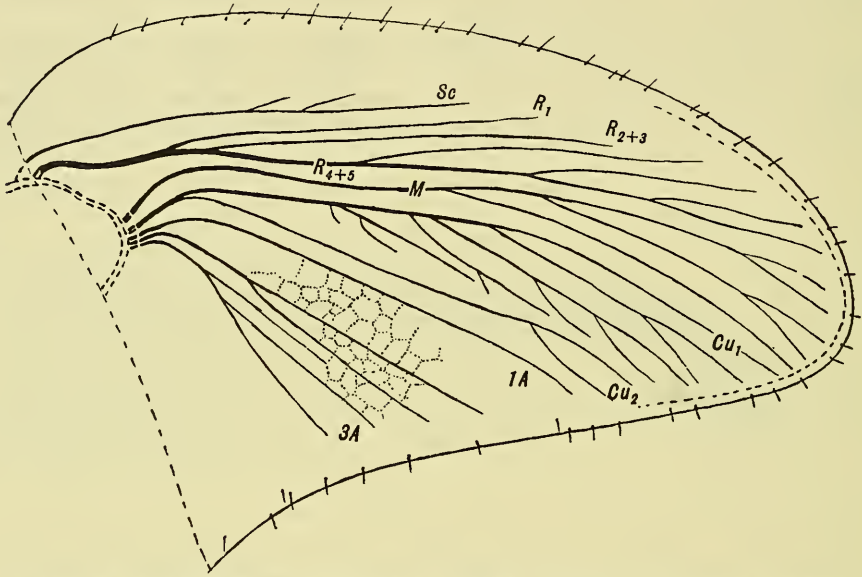


Text-fig. 1.—*Mastotermes darwiniensis* Frogg. Nymph, penultimate instar. Forewing, to show tracheation. Comstock-Needham Notation.

of the cubitus and anal veins; but the dissection cut across the origins of Sc, R and M. It was evident, however, that the tracheal trunk was stouter in diameter posteriorly than it is between the origins of Cu and the anal veins. This condition agrees closely with that found in a number of Cockroach nymphs, in which the original costo-radial and cubito-anal tracheal trunks are linked together into a complete loop by a middle connecting trunk of smaller diameter. In Text-fig. 1, I have restored the missing anterior portion of the trunk as on the supposition that it agreed with the Blattoid condition. Whatever may be the actual diameter of this trunk anteriorly, it is very clear that it formed a very deep loop, for this was the chief reason why I was unable to preserve it entirely in making the cut. As the cut left the main tracheae practically undisturbed in position, there is little difficulty in restoring the missing basal portions of Sc, R and M.

Text-figure 2 shows the tracheation of the hindwing of the same nymph as in Text-fig. 1. Here the breadth at base is enormous, even more than one-half the total length. The curvature of the wing-sheath, though marked, is not quite as

striking as in the forewing.  My attempt to include part of the basal trunk trachea
in the cut failed, although I made special efforts to reach the extreme base of Sc.
However, the cut was made very near the actual origins of all the main tracheae,
and I have given in Text-fig. 2 an approximate restoration of the position of the
basal trunk.

Before proceeding to a description of the wing-tracheae, it is worth noting
that the nymph dissected was evidently only in an early period of its instar,
and was therefore in excellent condition for dissection.   There was no rucking



Text-fig. 2.—*Mastotermes darwiniensis* Frogg.   Nymph, penultimate  instar.
Hindwing, to show tracheation.   Comstock-Needham  Notation.

or crumpling of the tissues, and the courses of the tracheae were consequently
very easy to follow.  The outline of the developing wing-sheath for the last instar
was only just beginning to show itself distally within the existing sheath, hence
my attempt to discover any indication of the limits of either the wing-stump of
the forewing or the anal lobe of the hindwing did not meet with any success.  An
interesting occurrence in the hindwing was, however, noted in the beginnings of
a sort of polygonal meshwork posterior to 1A.  It will be seen, later on, that this
area becomes secondarily invaded with branch tracheae from 1A, which is
originally developed as an unbranched trachea.

A comparison of Text-figs. 1 and 2 shows that, in both wings, only four main
tracheae exist in addition to the anal group.  In the forewing (Text-fig. 1), only
two short, rather weakly formed anal tracheae exist; in the hind (Text-fig. 2)
there are three, much more strongly developed.

This analysis of the system of main tracheae shows us at once that there
is no distinct costal trachea present in either wing.  Comstock himself recog-
nized this, so that we can safely reject the interpretations of Silvestri and
Holmgren, who consider that a separate costal vein was present in the imaginal
wing.

*The Subcostal Trachea.*—Apart from small anterior twigs, this trachea is usually unbranched in the hindwing (Text-fig. 2), hence there can be no difficulty in recognizing it. In the forewing, however (Text-fig. 1), its course is very arched basally, not far from its origin, and thus separated thereabouts quite considerably from the radial trachea posterior to it. Just distad from the arched portion, it gives off a basal anterior branch which is itself bifurcate. If this branch were constant, we should be justified in following Comstock's usual notation and designating it $Sc_1$. Unfortunately, however, it is not so. The examination of a series of imaginal forewings, as well as the study of the tracheation in the only available specimen of the last nymphal instar, indicates that the branching of Sc is highly variable, so that I consider it wiser to keep merely to the notation Sc for the complete trachea.

It may be noted, however, that this basal branch evidently occurs in a large number of forewings, and that it sometimes bifurcates even within the area destined to form the imaginal wing-stump; this was evidently the case in the nymphal wing here being studied, and also in the forewing figured by Holmgren (1911); he labels the corresponding portion of the venation "C".

The subcostal trachea ends distally less than half-way along the wing in the forewing, at about half-way in the hind.

*The Radial Trachea.*—As is to be expected, the radial trachea is the stoutest trachea in the whole wing. Moderately arched near the base in the forewing (Text-fig. 1), it runs for a space very close to both Sc and M, and then straightens out and runs the whole length of the wing to a point just above the apex. For the whole of its length, not a single posterior branch is given off; the whole system of branches of this trachea is anterior to the main trunk.

The first anterior branch is given off just as the trachea is straightening out after its basal arching. This branch is slender and runs just below and subparallel to the main stem of Sc, ending up only a little beyond it. Just distad from this branch, in the specimen under description, there arises another slender branch which bifurcates almost immediately, its two slightly diverging branches running to the costal border a little beyond half-way. Beyond this there are three more simple branches, subparallel to one another, then a shorter branch which bifurcates, followed by one more simple branch and a short terminal fork.

In the hindwing, the radial trachea arises closer to the subcostal, and has a general formation fairly closely similar to that of the forewing. The branches are, as in the forewing, all anterior, but they are only five in number and are all simple. It is interesting to note that, in both wings, the first two branches arise close together from the main stem.

The formation of the radial trachea, with its anterior system of branches, is a markedly Blattoid character. The normal type of radial trachea and vein, in other insects, is an anterior convex main stem, $R_1$, with a posterior concave sector, Rs, considered by Comstock to have been originally dichotomically divided into four branches, $R_2$ to $R_5$. While it is very doubtful whether Rs was originally either four-branched or dichotomically branched in the first winged insects, there can be little doubt that the division of R into an anterior convex $R_1$ and a posterior concave Rs is a primitive character, for it can be seen in nearly all known Carboniferous insects, including the Protoblattoidea, and is also well marked in some of the Carboniferous Blattoidea. The evolution of this latter group has, however, been along the lines of gradual recession of the area occupied by the subcosta and

invasion of that area by the radius.   Thus the original $R_1$, instead of being a long trachea or vein running very nearly to the apex (as in Mayflies, for instance), has followed the subcosta basad, and become shortened in the process to a mere anterior branch of Rs.   It has been followed in the same manner by $R_2$, $R_3$, $R_4$ and even by the more anterior branches of $R_5$; in the venation, each one of these, as it invaded the territory originally occupied by Sc, has tended to become more or less convex in conformity with the general convex tegminization of the wing.

If, therefore, we agree that the normal terminology of the Comstock-Needham system is applicable at all to the Blattoid type of radius, it is clear that only the most basal anterior branch can be considered as $R_1$, while all the rest of the radius must be considered as radial sector.   In so far as it is worth while to distinguish the parts further, the second anterior branch must be named $R_{2+3}$, and we may see in its bifurcate condition in the forewing (Text-fig. 1) evidence of its primitive dichotomy into $R_2$ and $R_3$, which has apparently disappeared in the hindwing (Text-fig. 2).   All the rest of the strong main stem is properly $R_{4+5}$, but only the most anterior branch of this can be assigned to $R_4$, while the remainder must be considered as $R_5$.   It follows that it will be most convenient to consider the main radial trachea and vein in Isoptera as simply the radial sector, distinguishing its most basal anterior branch only as $R_1$ if occasion arises.

*The Median Trachea.*—In the forewing this trachea arises just below the radius, but in the hind it arises far away from that vein and is associated purely with the cubito-anal group.   In both wings it is basally arched and then runs for some distance without branching.   The branches develop only from about half-way onwards, and are of the usual posterior type, but apparently with considerable variation in detail in individual wings, as may be seen by comparing Text-figs. 1–4. This variation renders any attempt to distinguish the four main branches postulated by Comstock and Needham more or less valueless, and it seems sufficient to recognize the median trachea as a whole, and simply to label it "M".

*The Cubital Trachea.*—This is the most characteristic trachea in the wing.   In both fore- and hindwings, it is divided into a strongly developed anterior branch, $Cu_1$, with a number of descending branches forming a pectinate series, and a much slenderer and simpler posterior branch, $Cu_2$, originating not far from the base and before the basal arching is complete.   This branch is either simple, as in the forewing in Text-fig. 1, or it may be terminally twigged as in the hindwing in Text-fig. 2.   A reference to the imaginal venation (Text-figs. 5, 6) will show at once that it is this trachea which follows the course of the *vena dividens* in the forewing and thus serves to divide the anal area from the main part of the wing; but equally, by reference to the hindwing venation, it will be seen that it lies far anterior to the anal lobe in that wing, and takes no part in delineating the anal fold there.

Comstock quite correctly interpreted the corresponding trachea in his figures of Blattoid nymphal wings (1918, pp. 124, 125, figs. 116, 117), but failed to homologize it correctly with the corresponding vein in the imaginal wing (l.c., figs. 118, 119).   Some of his followers have insisted on perpetuating this error and applying it generally to all types of wings, with the result that they destroy the whole basis of the Comstock-Needham system.   For it is the basic essence of that system that the veins of the imaginal wing should take their names from the tracheal trunks from which they are derived.   Now the vein which I here call $Cu_2$ has its trachea always arising from trachea Cu; hence, if it is to be called 1A, the whole basis of the system falls to pieces.   I have no objection whatever to

its being called CuP (posterior cubitus), as Lameere and Martynov propose, in which case the anterior cubitus should be termed CuA instead of $Cu_1$; but to term it 1A is absurd, when it is in no sense of the term an anal vein and is not derived from an anal trachea.

The question of objection to the use of terms such as $Cu_{1a}$ and $Cu_{1b}$ does not arise in considering the Isoptera, since $Cu_1$ is not dichotomically branched and there is little point in naming the individual branches of a variable pectinate series.

*The Anal Tracheae.*—In the forewing (Text-fig. 1) we distinguish clearly two anal tracheae, viz., 1A and 2A. Trachea 1A is delicately formed by comparison with the more anterior tracheae. It follows a very arched course, roughly concentric with the arched portion of Cu followed by $Cu_2$ above it, but diverging slightly from it distad. A short anterior branch runs in the curve of the arch between its main part and Cu. Trachea 2A is much shorter, arising just below 1A, equally delicately formed, and fills part of the space below the arch of 1A, branching irregularly into three.

Very different is the formation in the hindwing (Text-fig. 2). Here there appear to be three distinct anal tracheae, 1A, 2A and 3A, all arising close together and much better developed than in the forewing. 1A is an unbranched trachea running fairly close below and sub-parallel to $Cu_2$. Between it and the narrowly branched 2A there is a rather wide space, already noticed as carrying an initial development of irregular polygonal cells. A similar but less marked development of cells is indicated below 1A, between the two branches of 2A, and also distally just below 2A. Trachea 3A runs just below 2A, but branches somewhat earlier into three, the anterior branch being the shortest.
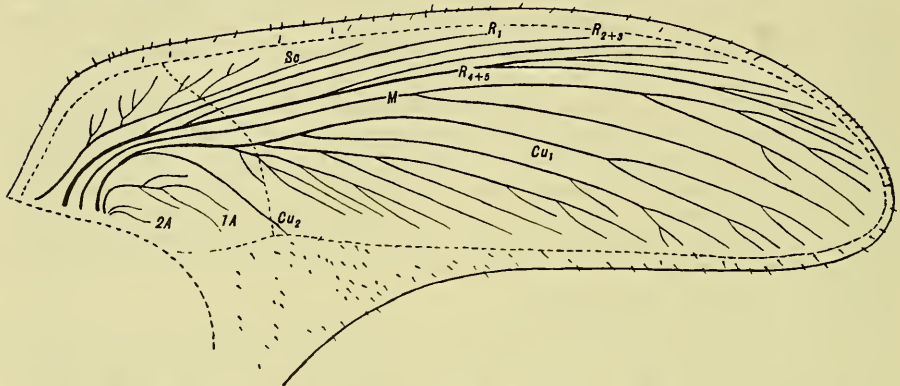
### (2) *The Wing-Tracheation of the Last Nymphal Instar.* Text-figs. 3, 4.

No living material of this instar has been available for dissection, but one nymph preserved in alcohol in Mr. G. F. Hill's collection was found to be in very good condition, having evidently been captured very soon after it had attained its final instar. A dissection of this showed the tracheae still *in situ*, so that I was able to make the drawings given in Text-figs. 3, 4, for comparison with those of the previous instar.

The chief difference to be noted in the shape of the wing-sheaths is their much greater elongation. The basal arching or bending is preserved, especially in the forewing. Fortunately the whole outline of the actual wings of the imago, in process of formation within the sheath, could be made out, and is shown by a fine dotted line in the figures. By following along the posterior margin, the distinct though slight inbending can be noted which marks the end of the *vena dividens* in the forewing and the anal fold in the hind. We then see quite clearly that these two formations are not homologous in fore- and hindwings; for the *vena dividens*, bounding the true anal area of the forewing, is obviously $Cu_2$ by comparison with Text-fig. 1, whereas the anal furrow in the hindwing runs along the course of the anterior branch of 2A!

There is no need to follow the courses of the tracheae in detail in this instar, but only to note the points in which they differ from those of the previous instar. In this particular forewing, the branchings of Sc are very irregular, consisting of four anterior veinlets, each of which is twigged. $R_{2+3}$ is unbranched, as in the hindwing in Text-fig. 2, but still arises close to $R_1$. The total number of anterior branches of R is rather markedly diminished; three branches, $R_1$, $R_{2+3}$ and

$R_{4+5}$, cross the suture of the wing-stump (Text-fig. 3). The first posterior branch of M arises a little before half-way. The general course of Cu is little altered, but $Cu_1$ is more arched near the middle of the wing, and most of the branches of its pectinate descending series tend to collect close together near the point where



Text-fig. 3.—*Mastotermes darwiniensis* Frogg. Nymph, last instar. Forewing, to show tracheation. Comstock-Needham Notation. The transverse dotted line indicates the position of the wing-suture.

this arching begins; they are also reduced in number, but are individually more branched than before. There is evidently very great irregularity in the form of these branches in individual wings.

Very notable is the reduction in size in $Cu_2$ and the anal tracheae. In the previous instar (Text-fig. 1) $Cu_2$ reached very nearly half-way along the wing; it now ends at little more than one-fourth. Also its course is now a still more definite arch than before. Within this arch can be seen the shortened and now quite irregularly branched trachea 1A together with a mere remnant of 2A in the form of two very short tracheae. At this early stage in the instar the outline of the
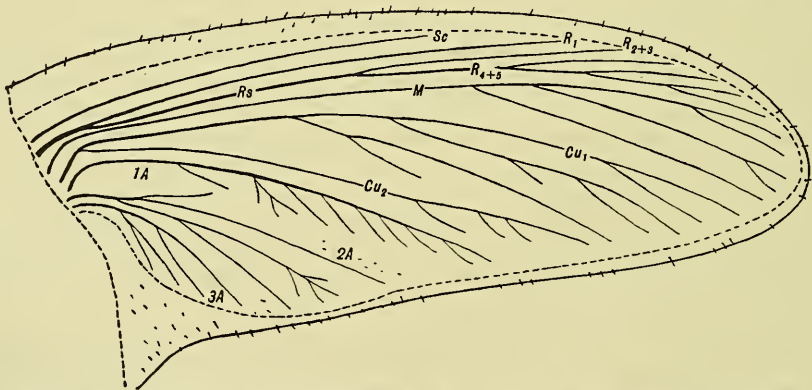


Text-fig. 4.—*Mastotermes darwiniensis* Frogg. Nymph, last instar. Hindwing, to show tracheation. Comstock-Needham Notation. The re-entrant angle of the posterior margin, indicating the limits of the anal lobe, is shown on the dotted line at the end of the trachea labelled 2A.

suture destined to separate the wing-stump from the rest of the wing cannot be clearly seen, but its future position can easily be inferred by reference to the imaginal venation, and is indicated in Text-fig. 3 by a dotted line traversing the basal quarter of the wing.

In the hindwing (Text-fig. 4) the changes are not great. Sc is now entirely without veinlets. Rs diverges slightly downwards after departing from $R_1$, thus tending to come very close to M. There is no important change in M and little in $Cu_1$ beyond a reduction in the number of descending branches. $Cu_2$ remains very long, reaching to a point about two-thirds along the posterior margin. 1A also remains long, and now sends a series of descending twiglets into the wide space in which we had noted, in the previous instar, a partial formation of a polygonal meshwork. Each of the two main branches of 2A has developed secondary branches; the main anterior branch of 2A runs along the course of the future anal fold, with the two well-formed branches of the posterior portion lying in the anal area below it. 3A is now four-branched, and supplies the lobed portion of the same area. The inbending of the posterior margin which indicates the termination of the anal fold lies at a point about two-fifths of the wing-length along that margin.

### (3) *The Venation of the Imaginal Wings.* Text-figs. 5, 6.

The study of the wing-tracheation of the last two nymphal instars has now prepared us completely for a full interpretation of the imaginal wing-venation. This is shown in Text-figs. 5, 6. The following points may be specially noted:

(1). In neither wing is there any evidence of the development of a true costal vein distinct from the subcosta. In the forewing, the short branches some-
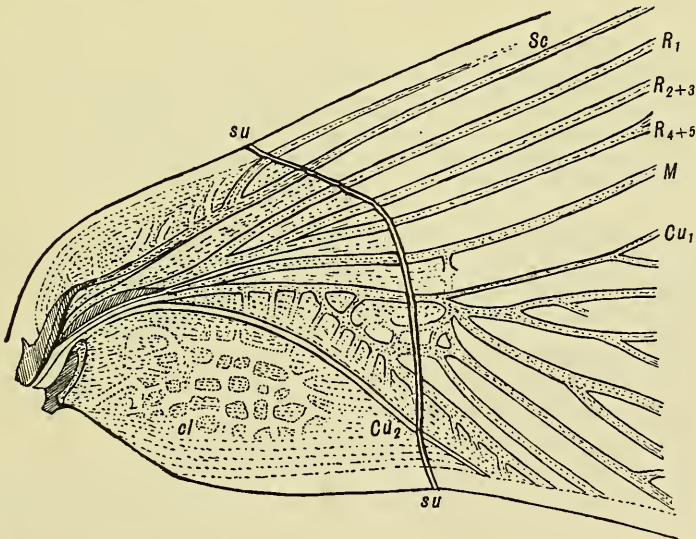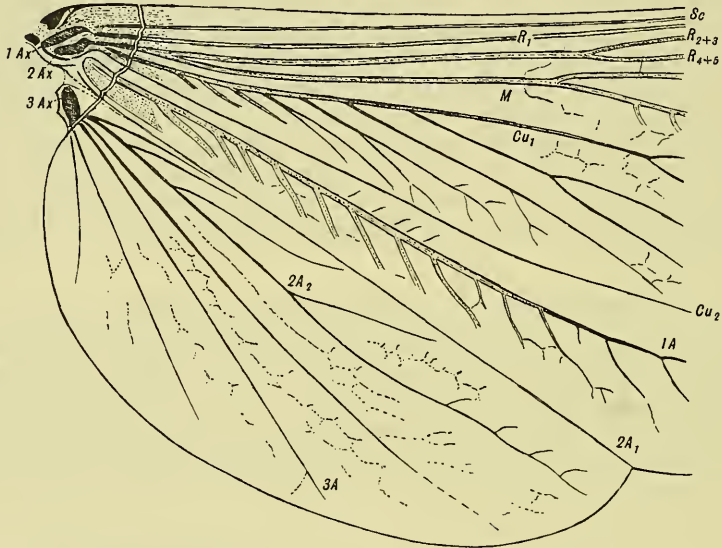


Text-fig. 5.—*Mastotermes darwiniensis* Frogg. Imago. Base of forewing, to show the wing-stump, the suture (*su*) along which the wing separates off at de-alation, the *vena dividens* ($Cu_2$) and the Blattoid form of the anal area or clavus (*cl*).

times found anteriorly within the wing-stump are properly to be considered as anterior branches of Sc, not as vein C.

(2). The main anterior longitudinal vein of the wing, with a number of anterior branches, is correctly termed the radial sector.  Its most basal anterior branch is the original $R_1$; there would appear to be little value, within the Order Isoptera, in naming the separate branches of Rs, as they are obviously very variable.



Text-fig. 6.—*Mastotermes darwiniensis* Frogg.  Imago.  Basal portion of hind-wing, including the whole of the anal lobe.  The line along which the wing breaks away at de-alation is shown by the double transverse lines close to the base (see also Text-fig. 7).  The three axillaries are labelled *1Ax, 2Ax, 3Ax* respectively, the last-named being separated from the other two by a thin membranous area.  $2A_1$, anterior convex branch of 2A which forms the anal fold.  $2A_2$, posterior branch of 2A with secondary anterior branches.

(3). No doubt exists as to the identity of vein M in the forewing.   The approximation of Rs near its origin from $R_1$ towards M in the hindwing of the last larval instar prepares us for its basal fusion with M in the imaginal hindwing. This character is universal in the Orders Isoptera and Perlaria.

(4). No doubt exists as to the identity of vein $Cu_1$ in either wing.  The more basal descending branches of this vein tend to flatten out in the forewing, and within the wing-stump they are partially atrophied.  In the hindwing, they also tend to stop short in the membrane as they approach $Cu_2$.

(5). The *vena dividens* in the forewing is a weakly chitinized concave vein and forms the anal furrow.  It is undoubtedly $Cu_2$.  In the hindwing, the homologous vein is also very lightly chitinized, but lies far anterior to the anal fold.

(6). The anal area or clavus of the forewing is of the strongly arched Blattoid type.  The anal venation has degraded, and is replaced by an irregular polygonal meshwork, usually very faintly indicated.

(7). The anal lobe of the hindwing is not coterminous with its anal area, but is remarkable in being bounded anteriorly by the most anterior branch of 2A, which in the imago is barely chitinized and forms the anal fold. Vein 1A, lying anterior to the lobe, tends to duplicate $Cu_1$ in form, but somewhat on a reduced scale, through the formation of hypertrophied descending branches which stop short before reaching 2A. The branchings of the posterior main branch of 2A and also of vein 3A within the anal lobe are highly irregular, and an indefinite polygonal meshwork is developed between them. At the base of the wing, the third axillary (Text-fig. 6, *3Ax*) is seen to be well separated from the first and second axillaries (*1Ax, 2Ax*) by an area of thin membrane; the veins 2A and 3A spring directly from the third axillary.

It should be noted that the anal fold of the hindwing is a convex fold, the anal lobe folding along it beneath the rest of the wing. The *vena dividens* of the forewing, on the contrary, is a concave furrow (anal furrow of Comstock). It is therefore unfortunate that Comstock applies the same terminology, "anal furrow", to both these structures.

As regards the exact composition of the vein M, according to Lameere's terminology, I have so far said nothing. The position would appear to be similar to that in the Blattoidea, where, so far as I am aware, there is no evidence of a division into distinct anterior median (convex) and posterior median (concave) at all. Tegminization of the forewing in the Blattoidea has made all the veins except $Cu_2$ appear more or less convex; but a reference to the hindwing, as well as to both wings in the Mantoidea, makes it fairly certain that the media is really only the posterior median, MP, of Lameere. Whether an original anterior median, MA, has taken any part in the formation of the vein which we now call the radial sector is a question which must for the present be left open. To determine this, we need clear evidence as to what group of Blattoidea or Proto-blattoidea are the actual ancestors of the Order Isoptera. Such evidence, at present, appears to be entirely lacking.

That the Isoptera are closely related to the Blattoidea is now quite certain, and this conclusion is still further strengthened by the present study. We have now to decide whether the family Mastotermitidae lies along the direct ancestral line or not. The main difficulty lies in the interpretation of the anal lobe.

In all Blattoidea and Mantoidea the folded portion includes the whole of the anal venation, whereas, in *Mastotermes*, 1A lies wholly outside the folded portion, and the folding itself takes place along the anterior branch of 2A. This fact may be interpreted in one of two ways: either *Mastotermes* is descended from ancestors which, like all other Isoptera, entirely lacked the folded anal area, and, later on, a secondarily enlarged folded area has been developed with a different boundary, or else *Mastotermes* exhibits a reduction-stage in the transition from the normal Blattoid or Mantoid type of hindwing to the normal lobeless type of the rest of the Isoptera, the reduction having been effected by the trans-ference of vein 1A from the original folded area on to the unfolded portion of the hindwing.

All the evidence appears to me to favour the second supposition. In the original Blattoid and Mantoid type of hindwing, $Cu_2$ is a long and weakly chitinized concave vein, forming the *vena dividens* which separates off the anal area from the rest of the wing. Running closely below it is the convex vein 1A, along which the actual underfolding of the anal lobe takes place. Usually there is a break in

the form of a re-entrant angle in the posterior margin at the end of $Cu_2$; but there are many Mantoid types in which the contour of the posterior margin is continuous, and some Blattoids in which the break is only very slight.    The development of the condition found in *Mastotermes* from the normal Blattoid condition requires (*a*) the elimination of the re-entrant angle at end of $Cu_2$, so that the posterior margin should form a continuous curve, (*b*) the possession, in the ancestral form, of a branched 2A, and (*c*) reduction of the folded area by trans-ference of vein 1A on to the unfolded portion, the secondary folding taking place instead along the line of the anterior branch of 2A.  We have already seen that condition (*a*) offers no obstacle to the theory that *Mastotermes* lies in the direct ancestral line.   As regards condition (*b*), it is sufficient to note that 2A is normally branched both in Blattoids and in Mantoids, and there are many types in which the development of a long anterior branch, itself simple and suitable to function as a secondary anal fold, is obviously quite possible.  Condition (*c*) would then be fulfilled, most probably, if, during the course of evolution, there were to take place a disproportionate change in the length of the veins, as, for instance, in the event of an inordinate lengthening of the wings.  Such a lengthen-ing would carry the original *vena dividens* far out beyond the end of the abdomen of the insect, as has actually happened in the case of *Mastotermes*, with the result that the folded area would no longer be entirely protected beneath the body.  If the manner of folding were to remain the same, i.e., about a convex fold, it is clear that the next position suitable for folding must develop along the first branch of 2A, as has happened in *Mastotermes*.

Now the length of the forewing in *Mastotermes* is about 30 mm., that of the hindwing about 28 mm.  The abdomen, however, is only 10 mm. or somewhat less, and the distance from the base of the hindwing on the metanotum to the end of the abdomen is about 12 mm., which is the same as the length of the anal fold.  Thus the folded portion, when in the position of rest, fits neatly over the abdomen, and does not project beyond it so as to risk tearing.  I think it will be admitted that the length of the wings in *Mastotermes*, and, indeed, in all Isoptera, is out of all proportion to the length of the abdomen, and that very definite elongation of the wings must have taken place at some stage in the evolution of the Order.   Therefore it appears that a clear case has been made out for the view that *Mastotermes* lies in the direct ancestral line of the evolution of the Order, and retains an intermediate condition in the reduction of the folded anal area by transference of the actual fold from the convex vein 1A to the convex anterior branch of 2A.

### (4) *The Problem of De-alation.*

De-alation is the process of shedding the wings.   In the high development of this process, the Order Isoptera is the most specialized of all Orders of Insects.

In the Isoptera, alate individuals of both sexes normally shed their wings at some period after their emergence.  But there is a great deal of difference between the lengths of time usually taken before de-alation occurs in different groups, and also in the ease with which the wings are shed.  Normally, however, both pairs of wings are shed with equal ease.

The small basal portion of the wing which is left attached to the thorax, after de-alation has taken place, has been called the wing-stump, wing-stub or wing-scale by various authors.  The last of these expressions is the one most commonly in

use; but it is open to the serious objection that it is already in use for an entirely different structure, viz., the wing-scales of butterflies, moths, mosquitoes and other insects. I therefore propose to use the term wing-stump in this and subsequent papers, since that term exactly describes the piece of the wing which is left behind, and is not in use for any other structure.

Normally, the fully developed wings of Isoptera have a transverse line of weakness, the basal suture (Text-fig. 5, *su*), clearly marked between the wing-stump and the remainder of the wing. The insect gets rid of its wings merely by pushing or rubbing against any convenient rough surface, or by some action which causes bending of the wings at the sutures, such as raising the abdomen, or raising the thorax high on the legs so that the tips of the wings press against the ground or object on which the insect is standing. In the majority of cases, even very moderate pressure or displacement is sufficient to rupture the wing along the suture, and de-alation results at once. But, as will be seen later when we come to study other groups of Isoptera, there are some cases in which the wings are not so easily shed.

As de-alation is a highly specialized phenomenon, and is better developed in the Isoptera than anywhere else, it appears reasonable to suppose that characters of considerable value in a scheme of classification for the Order ought to be found in connection with it. I propose, therefore, to consider the nature of the wing-stump and basal suture in the various families of Isoptera, together with the differences which may exist in them in the fore- and hindwings.

The Mastotermitidae differ from most other Isoptera in the fact that, while the forewing possesses a well-developed basal suture and large wing-stump (the latter measuring in length about one-ninth of the total length of the wing), the hindwing does not appear to show any sign of a true suture at all. Further, living specimens have frequently been found in which the forewings have been shed whilst the hindwings have been retained. It is true that, in the end, both pairs of wings are shed; but it is also true that the hindwings are often retained much longer than the fore.

If a winged specimen of *Mastotermes* be taken out of alcohol and held in the fingers or by the forceps, it can easily be verified that a slight pushing or bending of the forewing will cause the wing to split along its basal suture, which is always very clearly marked. The crack appears first inwards from the costa across Sc and R, and then opens up rapidly as far as $Cu_2$. From this vein to the posterior margin is only a small distance; yet this part does not yield as readily as the rest, and the final tear may either take place obliquely along the course of $Cu_2$, or it may continue the transverse course already begun, leaving the tip of $Cu_2$ itself on the de-alated portion of the wing. An examination of specimens de-alated naturally while alive shows that the latter method is by far the most usual. Occasionally, however, one sees the oblique tear along the course of $Cu_2$. Occasionally, also, it happens that the suture runs to the posterior margin either exactly at the end of $Cu_2$, or even slightly distad from it. In the latter case, the whole of vein $Cu_2$ is left on the w.ng-stump, as is the case with the forewings of other families of Isoptera known to me. In the majority of specimens examined, the distal part of $Cu_2$ lies just beyond the wing-stump, as in Text-fig. 5.

Now if we try to remove the hindwing of a specimen of *Mastotermes* taken from alcohol, we shall find that it is by no means as simple a task as in the case

of the forewing. One can press the wing forward towards its base with quite considerable force, and still obtain no result. However, if sufficient buckling of the wing can be obtained, a split will occur close to the base, from costa to Sc only, and nearly at right angles to the former. If, now, further bending or pushing is continued, this split can be made to open up transversely across the other veins, as far as the end of the chitinized block which lies at the base of 1A. Owing to the separation of the third axillary (Text-fig. 6, *3Ax*) from the other basal chitinized structures of the hindwing, the attachments of this wing to the thorax consist of two blocks of fairly hard chitin separated by a thin membrane in the region of the anal fold. In following out the progress of the split, it will thus be seen that it has now reached a point impinging upon the anal fold itself. Along this same fold the hindwing, in the position of rest, is folded in such a way that the anal lobe lies beneath the rest of the wing. If the pushing or bending of the wing is continued still further, the next result will either be that a tear will take place along the anal fold, or irregularly across the anal lobe, or it may happen that the original split will be continued across the anal fold and follow an irregular course across the other anal veins. If the transverse splitting is continued in this last manner, as shown in Text-fig. 6, then the branches of 2A and 3A will be found to be severed practically at their origins with the third axillary, where they are weakly chitinized. This appears to be what usually happens in nature. But it would be worth while to examine a large number of naturally de-alated individuals, in order to determine what percentage of them do actually succeed in ridding themselves completely of the anal lobe of the hindwings.

Two important characters emerge from this study of the process of de-alation. The first is that the forewing possesses a definite basal suture, while the hindwing does not. The second is that the wing-stump of the forewing is much larger than that of the hind. The first character is one in which the Mastotermitidae differ from all other Isoptera studied by me. It is obvious that the sutureless condition of the hindwing is an archaic character, and that it is at any rate partly correlated with the preservation of an anal lobe. The second character does not serve to distinguish the Mastotermitidae from the more archaic groups in the rest of the Order, e.g., the Calotermitidae, in which also we may note a marked difference in the size of the wing-stumps of fore- and hindwings.

It does not seem likely that we can definitely prove the method whereby the living individuals of *Mastotermes* rid themselves of their hindwings, except by actual observations on living specimens before de-alation. But a study of the two wing-stumps *in situ* is very suggestive. If we take a specimen from alcohol and remove its forewings, which can be done with ease, and also without injury to the hindwings, then we note, first of all, that the wing-stump of the forewing is slightly convex, and that it presses down firmly upon the base of the hindwing. The suture between metathorax and abdomen lies slightly distad from the free edge of the fore wing-stump. There appear, then, to be two fulcral lines along which the hindwing might be bent and split in nature; the first would be along the hard edge of the fore wing-stump, while the second would be slightly distad from this, just over the suture between thorax and abdomen. Experimentally, I have succeeded in inducing splitting along both these lines, but it is much easier to do it along the hard edge of the fore wing-stump than along the other position. If the hindwing be simply seized with the forceps and bent upwards against the fore wing-stump, it will split along the line of bending, at any rate as far

as the anal fold. But to achieve the second result, it is necessary for the abdomen to be raised upwards until the hindwing is actually caught between the concavity of the suture between thorax and abdomen below it, and the sharp edge of the fore wing-stump above it; when that happens, a similar split takes place, but slightly distad from the line of the fore wing-stump. This operation cannot be done easily with a specimen taken from alcohol, owing to loss of elasticity in the abdomen. But it is conceivably quite an easy operation for the living insect.

Examinations of specimens taken alive in the de-alated condition, from Mr. Hill's collection, indicate that, in all cases, the split in the hindwing is placed slightly distad from that of the fore. This can be well seen in Text-fig. 7. This fact may be interpreted either as proving that the second method of de-alation, mentioned above, is the actual process employed in nature, or it might still be argued that it is the first method that is employed, and that subsequent swelling of the tissues during immersion in alcohol has caused the displacement now noticeable. Mr. Hill, however, informs me that, in preserving his specimens, he changed the alcohol frequently, after death of the specimens, for the express purpose of avoiding distension of the body tissues. My impression, after studying a considerable number of his specimens, is that no appreciable change in the position of the thoracic structures has taken place. Therefore I strongly incline to the second explanation, as stated above. But, as I said before, the actual proof of this point must await observations in the field.

Let us now return to our study of the naturally de-alated specimen, as shown in Text-fig. 7. Under the microscope, the difference in the natures of the distal



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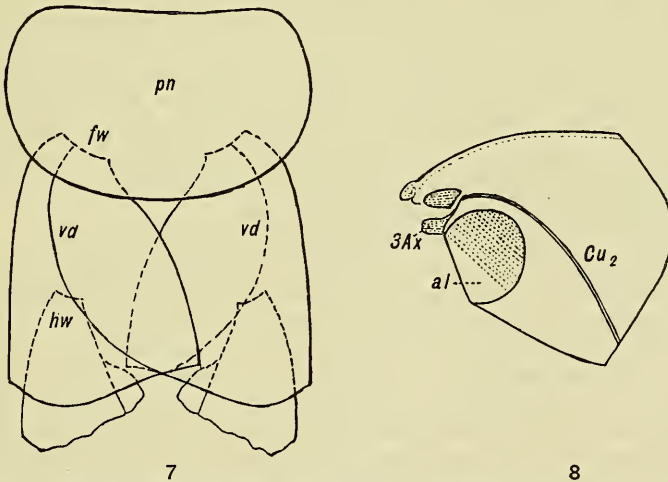
Text-fig. 7.—*Mastotermes darwiniensis* Frogg. Diagram of part of imago, to show the pronotum (*pn*) with the wing-stumps in position after de-alation. *fw, hw,* bases of attachment of forewing to mesonotum and of hindwing to metanotum; *vd, vena dividens.* Note the close alignment of the severed ends of the two pairs of wings, and also the alignment of the *vena dividens* with the severed ends. The parts which are covered by other structures are shown by dotted lines; the left forewing overlies the right, and both forewings overlie the hindwings. The posterior part of the lobe of the pronotum overlies the bases of the forewings.

Text-fig. 8.—Diagram of forewing-stump, viewed from beneath, to show position of alula (*al*). 3*Ax,* third axillary; $Cu_2$, *vena dividens.*

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margins of the two wing-stumps can be easily made out.   In the forewing, there is no sign of tearing; the main veins are all clearly weakened at the points where they impinge upon the suture, and the intervening membrane is also neatly separated along the sutural line, not torn off roughly.   But in the hindwing, the main veins are evidently broken off, while the intervening membrane is torn off irregularly between them.   Thus the distal margin of the fore wing-stump is fairly regular, while that of the hind is more or less jagged.

Measurements of the two wing-stumps show that, whereas that of the fore-wing is about one-ninth of the total length of the wing, that of the hindwing is not quite one-sixteenth of the total length.   In actual area, the wing-stump of the forewing is much greater than that of the hind, since it is wider as well as much longer.   A careful calculation gives the ratio of the areas as about 8:3.   Striking as these differences are, they are nevertheless exceeded in some genera belonging to the Calotermitidae.

For purposes of comparison with other groups, we have also to bear in mind the markedly Blattoid form of the clavus or anal area of the forewing in *Masto-termes*.   This is undoubtedly a very primitive character; so far as I know, it is unique within the Order Isoptera.   The Blattoid form of clavus is due chiefly to the marked curvature of vein $Cu_2$ concavely to the posterior margin.   Even in those Calotermitidae in which the form of the fore wing-stump most closely approaches that of *Mastotermes*, it will be seen that this concave curvature of vein $Cu_2$ has been lost.

Another character which appears to promise well for comparison with other groups is the actual course of the split in both wings.   In the forewing of *Mastotermes*, it runs obliquely downwards and outwards from the costa as far as $R_{4+5}$, then turning to run transversely as far as $Cu_2$, whence it turns slightly out-wards to reach the posterior margin.   Such a course may be described as convex to the base, with its principal bend or angle on or near $R_{4+5}$.   The course of the split in the hindwing (which, we have already shown, is not a true suture in *Mastotermes*) is also convex to the base, with a slight bend or angle at Sc, and thereafter somewhat irregular.   Deviations from this primitive type will be care-fully noted in our studies of the higher families.

*The Alula of the Forewing* (Text-fig. 8).—During the examination which I made of the process of de-alation, I lifted up with the flat blade of a scalpel a complete forewing of a specimen of *Mastotermes* taken from alcohol.   In this case, the wing did not break as easily as usual at the suture, and I succeeded in raising it to an angle of about sixty degrees from the body.   I was then extremely surprised to see standing out at a slight angle beneath the extreme base of the wing a small lobe, which at once reminded me of the alula of the Coleopterous family Hydrophilidae.   Carefully slipping the scalpel along beneath this, I sliced the wing off below it.   The wing was then turned over and examined in alcohol and a drawing of the alula made (Text-fig. 8).   It consists of a more or less rounded flap, joined to the basal part of the clavus by a wide chord or base of attachment, the anterior end of which is very close to the third axillary.   The free rounded part of the alula is more or less deeply pigmented in brown, but a rather triangular area in contact with the base of attachment is so completely hyaline as almost to escape detection at first sight.   The alula folds closely under the clavus, its outer margin not reaching as far as the *vena dividens*.   It thus bears much the same relationship to the clavus of the forewing as the anal lobe of the hind bears to the rest of the anal area of that wing.

It seems strange that this structure should have previously escaped detection, but such appears to be the case. In order to make sure that I was not mistaken, I asked Mr. Tonnoir to dissect another forewing from a specimen of *Mastotermes* in the same manner, and he discovered in this specimen a similarly placed lobe, an undoubted alula, which only differed from the one found by me in being slightly smaller and more oval in form, and had the same hyaline appearance at the base.

We may therefore take it as proved that there is a true alula of the type found in certain Coleoptera in the forewings of *Mastotermes*. The structure should be searched for also in other primitive genera of Isoptera, and will very probably be discovered, perhaps in an obsolescent form, in some of them.

Whether this curious structure has any phylogenetic significance or not, I am not prepared to say at the present moment. The Hydrophilidae are admittedly a very archaic family of Coleoptera, but it does not yet appear to be established that the alula was present in the ancestral type of elytron for that Order. If that were so, then the presence of a similar organ in *Mastotermes* might be held to indicate a community of origin for the Orders Isoptera and Coleoptera. This problem, however, lies beyond the scope of the present paper.

### Summary of the Characters of the Wings in the Family Mastotermitidae.

We are now in a position to define the family Mastotermitidae on the characters of its wings, as follows:

*Forewing.*—Wing-stump large, its length measured from the base along vein M being about one-ninth of the total length of the wing. Wing-suture convex to base, with a bend or obtuse angle about vein $R_{4-5}$. Anal area or clavus of Blattoid form, with the *vena dividens* ($Cu_2$) curved concavely to the posterior margin; normally, this vein is not quite fully included within the wing-stump, a small distal portion of it remaining outside. A true alula present in the form of a small rounded flap attached along a broad base at the base of the clavus, and folded completely under it. Venation almost complete, with branched Sc, many-branched R, M and $Cu_1$; $R_1$ and $R_{2-3}$ simple, $R_{4-5}$ with many anterior branches; anal veins obsolete and replaced by a very variable, indistinct and irregular meshwork, frequently obsolescent also.

*Hindwing.*—Wing-stump small, its length being less than one-sixteenth of the total length of the hindwing. No true wing-suture present, but the wing splits or tears off at a level slightly distad from the position of the free edge of the fore wing-stump in the position of rest (Text-fig. 7). A large anal lobe present, formed with the convex anterior branch of vein 2A as the anal fold; length of this lobe, measured along 2A, quite two-fifths of the total length of the wing. The anal lobe folds under the rest of the wing along the anal fold and may be strictly homologous with the alula of the forewing. Venation complete, with Sc simple or forked, $R_1$ and $R_{2-3}$ simple and $R_{4-5}$ with many anterior branches, as in forewing; but at its extreme base Rs is fused for a short distance with M; M and $Cu_1$ many-branched, $Cu_2$ simple or only forked distally. Anal veins well developed; 1A stout, with a series of irregular descending branchlets; 2A forked completely from base, the anterior branch lightly chitinized and forming the anal fold, the posterior branch with anterior branchlets; 3A with several branches arising from the third axillary.

Membrane of both wings thin and covered with a weak, irregular meshwork of veinlets, or archedictyon.

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### EXPLANATION OF PLATE XXI.

*Mastotermes darwiniensis* Froggatt.—Enlarged photographs of fore and hind wings, from specimens dissected off with wing-stumps attached, and cleared and mounted in euparal.

Photographs by W. C. Davies, Cawthron Institute, Nelson, N.Z.

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